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Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments

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Abstract

Bottom-trawl fisheries are wide-spread and have large effects on benthic ecosystems.We investigate the effect of scallop dredging on sand and otter trawling on mud by measuring changes in the infaunal community and the biogeochemical processes which they mediate. We hypothesize that changes in biogeochemistry due to fishing will be larger in mud where macrofauna-mediated processes are expected to play a greater role, than in sand where hydrodynamics mediate the redox system. We sampled benthic infauna, sediment porewater nutrients, oxygen, chlorophyll *a* (Chl *a*), apparent redox potential discontinuity layer, organic carbon and nitrogen content over a gradient of fishing intensity in sand and mud. The effects of fishing on biogeochemistry were stronger on mud than on sand, where biogeochemistry appeared to be more strongly influenced by tidal currents and waves. On mud, trawling increased sediment-surface Chl *a* and ammonium concentration beyond 5 cm depth, but decreased ammonium and silicate concentration in the upper sediment layers. The effects of fauna and bioturbation potential on biogeochemistry were very limited in both mud and sand habitats. Our results suggests that otter trawling may be affecting organic-matter remineralization and nutrient cycling through sediment resuspension and burial of organic matter to depth rather than through the loss of bioturbation potential of the benthic community. In conclusion, our hypothesis that the effects of trawling on biogeochemistry are larger in mud is supported, but the hypothesis that these effects are mediated by changes in the infauna is not supported. These results imply that management of trawling on muddy sediments should have higher priority.

Fishing with bottom towed fishing gear is a major source of physical disturbance for marine benthic ecosystems. Large parts of most shelf and deep seas have been intensively exploited by bottom fishing for decades (Halpern et al. 2008; Puig et al. 2012). As nets, beams, trawl doors, chains and dredges pass over the seabed, the sediment surface is disturbed and 20–50% of the resident biota (e.g., bivalves, burrowing crustaceans, tube-building polychaetes, and echinoderms) is damaged or removed (Jennings and Kaiser 1998; Kaiser et al. 2006). Previous studies have shown that bottom fishing results in a decrease in benthic secondary production, as well as changes in the community structure and size composition of benthic invertebrate communities (Hiddink et al. 2006; Hinz et al. 2009; Bolam et al. 2014a). Shifts toward higher abundances of scavenging and deposit feeding organisms and small-bodied infaunal species have also been reported due to trawling (Kaiser et al. 2000; Tillin et al. 2006).

In addition to changes to benthic faunal communities, bottom fishing can alter the biogeochemical characteristics of the sediment and that of the overlying water column through a combination of the removal of surficial sediments and the burial or mixing of organic matter (Duplisea et al. 2001; Warnken et al. 2003; O'Neill and Summerbell 2011). The resuspended sediment created by groundropes, chains and nets as bottom trawls are dragged along the seabed increases the water turbidity and the concentration of particulate organic matter in the overlying water and may enhance phytoplankton primary production due to higher nutrient loads (Riemann and Hoffman 1991; Pilskaln et al. 1998; Palanques et al. 2001). Changes within the sediment matrix, such as an increase in sediment sorting and porosity (Trimmer et al. 2005) can result in changes to the oxygen

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Additional Supporting Information may be found in the online version of this article.

regime (Warnken et al. 2003), which may influence key steps in the nitrogen cycle, as oxygen regulates both nitrification and denitrification in benthic sediments (Rysgaard et al. 1994). Because of their weight, otter trawl boards and dredges create large furrows in the sea floor that range between 5 cm and 35 cm deep depending on the type of sediment (Eigaard et al. 2015). The redistribution of organic matter that results from this ploughing action may shift the balance between aerobic and anaerobic mineralization, as the organic matter is buried beneath the narrow oxic zone before mineralization is complete (Mayer et al. 1991; Pilskaln et al. 1998). Duplisea et al. (2001) and Trimmer et al. (2005) found higher rates of organic matter remineralization via sulphate reduction at high trawling disturbance areas.

Indirectly, bottom fishing may affect the oxygen regime and biogeochemical processing of carbon by altering the composition of the benthic fauna, which itself regulates oxygen and redox structure through bioturbation and bioirrigation (Kristensen 2000; Duplisea et al. 2001; Waldbusser et al. 2004). Mesocosm experiments by Olsgard et al. (2008) showed that the reduction of large-bodied bioturbators such as the surficial modifiers *Brissopsis lyrifera* and *Nuculana minuta*, resulted in a lower efflux of silicate (SiO_4^-) and nitrate/nitrite (NO_x) from the sediment to the overlying water. Declines in the density of burrow- and tube-building organisms may result in changes to benthic respiration and denitrification due to a reduction in oxygen penetration and microbial metabolism (Aller and Aller 1998; Braeckman et al. 2010). It may therefore be expected that trawling will affect sediment chemistry through a reduction in community bioturbation potential, burrow density and functional diversity.

Habitat characteristics may be strong determinants of the relative impact of bottom fishing activity on both the infauna and sediment biogeochemical processes. For example, the effects of bottom fishing on benthic carbon mineralization and sediment characteristics (e.g., particle size distribution, porosity) have been demonstrated to be smaller in highly natural disturbed areas where wave and tidal actions lead to bulk sediment disturbance and transport (Osinga et al. 1996; Trimmer et al. 2005). Similarly, several studies have shown that the effects of fishing on fauna are smaller in coarse than fine sediment (Collie et al. 2000; Kaiser et al. 2006; references therein), as the former are characterized by a higher fraction of small-sized, fast growing and highly productive species that are more adapted to continual natural disturbance by tides and waves (Kaiser and Spencer 1996). Experiments have shown that the influence of bioturbation on nutrient regeneration and oxygen consumption is greater in diffusion dominated (low disturbance, fine sediments and low rates of sediment pore water exchange) than in advection dominated (high disturbance, coarse sediments and consequently high rates of sediment pore water exchange) systems, as sediment processes in the former are more strongly influenced by bioturbation (reviewed by Mermillod-Blondin and Rosenberg 2006). It may therefore be expected that trawling disturbance will have stronger effects on the fauna and biogeochemical processes in mud than on sand by altering diffusion of dissolved oxygen from the sediment-overlying seawater into the pore water and oxygenation of the sediment pore water by sediment resuspension.

Few empirical studies to date have investigated the combined effects of bottom fishing on both the infaunal community and the biogeochemical processes which they mediate (Pilskaln et al. 1998; Duplisea et al. 2001; Waldbusser et al. 2004; Hiddink et al. 2006), and this is important for understanding the impacts of fishing on ecosystem functioning. This study fills this knowledge gap by assessing the large-scale impact of chronic bottom fishing on benthic community structure and sediment biogeochemistry across different fishing pressure gradients and habitat types (muddy vs. sandy habitats). The following hypotheses are tested; (i) fishing will negatively affect benthic invertebrate abundance and reduce the bioturbation potential of the community as large bioturbatory macrofaunal species are removed by trawling; (ii) fishing will result in changes in the sediment redox and associated biogeochemistry as a result of sediment resuspension (e.g., lower concentration of NH_4^+ in upper sediment layers) and sediment/carbon mixing to depth (e.g., higher concentration of NH_4^+ in pore-water); (iii) changes in sediment biogeochemistry due to fishing will be larger in mud where macrofauna-mediated processes are expected to play a more significant role, than in sand where physical processes such as tides and currents generally mediate the redox system.

Methods

The effects of chronic bottom fishing on benthic infauna and sediment biogeochemistry were investigated over gradients of commercial bottom fishing intensity on muddy and sandy fishing grounds in the north Irish Sea between the 28th June and 6th July 2014 (Fig. 1). The sandy fishing ground was located off the east coast of the Isle of Man where scallop dredging for *Pecten maximus* and some otter trawling for *Aequipecten opercularis* occurs. Scallop dredging occurs between May and November, whereas otter trawling occurs between June and October (Murray et al. 2010; Dignan et al. 2014).Within the Isle of Man territorial waters trawling is traditionally conducted by vessels fishing with single rig otter trawls with net openings of 18–32 m (Dignan et al. 2014). Scallop dredgers are allowed a maximum number of 8 dredges per side, with a maximum number of 9 teeth per dredge each 110 mm in length (Murray et al. 2010). The muddy fishing ground was located off the coast of Cumbria, England, where otter trawling for *Nephrops norvegicus* and gadoid fish occurs. The fishery operates throughout the year with a peak activity from spring to early summer (Hinz et al. 2009). Vessels are limited to operate otter trawls with a maximum headline length of 9 m

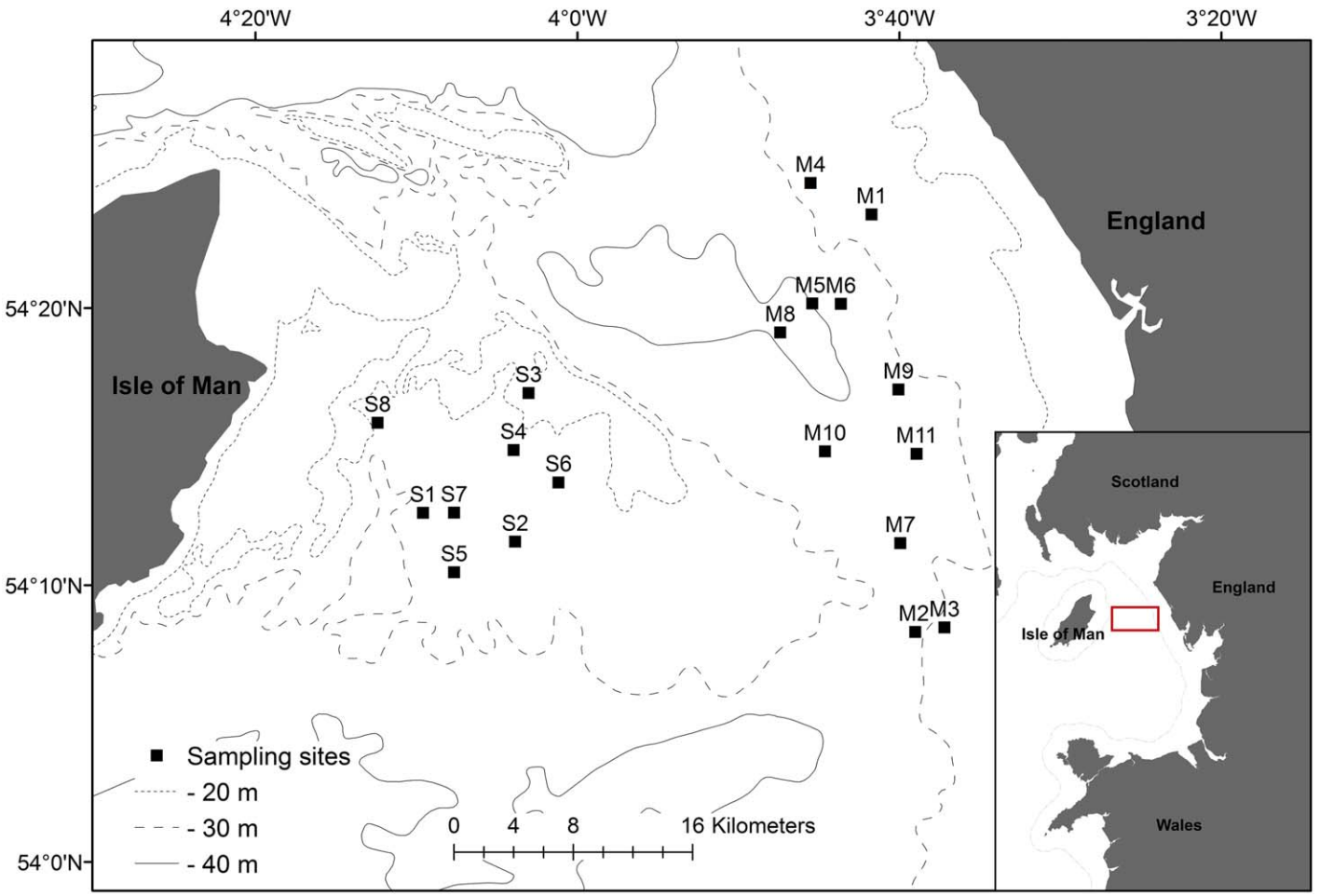

Fig. 1. Map of the sampling sites at the sandy sediment location (Isle of Man fishing ground, S1–S8) and the muddy sediment location (*Nephrops* fishing ground, M1–M11).

(NWIFCA 2013 pers. comm.). These areas were selected because both of them showed a spatial gradient in fishing pressure within areas of homogenous sediment types (Supporting Information SM 1). Other habitat characteristics were similar between the two areas (water depth, bottom temperature, and tidal currents) (Supporting Information SM 1).

Station selection

Within each of the two areas, sixteen 1 × 2 km sites were selected along a gradient of fishing pressure. Sampling site selection was based on existing knowledge of sediment type and water depth (CEFAS, unpubl. data and information available in British Geological Survey maps) and natural tidal and wave bed-stress to ensure comparability. The average (± SE) water depth at the muddy study sites was 35.5 ± 3.8 m, while that at the sandy sites was 26.3 ± 4.0 m (Supporting Information SM 1). Bed shear stress was used as a measure of natural disturbance to quantify tidally generated currents and wave action that affect sediment transport by advection and hence the structure of the invertebrate community. Estimates of the mean tidal- and wave-bed shear stress (Nm^{-2}) at the study sites were derived from a two-dimensional hydrographical model of the Irish Sea (detailed description on shear stress calculations in Hiddink et al. 2006), and ranged between 0.11–0.25 Nm^{-2} and 0.4–1.4 Nm^{-2}, respectively (Supporting Information SM 1).

The fishing pressure at each of the 32 stations was estimated by computing the accumulated swept areas within a year from all the bottom-contact fishing gears (otter and bottom pair trawls, scallop dredges) by vessels larger than 15 m registered to fish in UK waters. In order to obtain a measure of the chronic disturbance experienced at the two study areas, fishing pressure estimates were calculated from Vessel Monitoring System (VMS) data averaged over a 3 yr period before the study was conducted. At the time of site selection, VMS data for the period January 2009 to December 2011 were available for the sandy study area and for the period January 2010 to December 2012 for the muddy study area. VMS data were combined with logbook data (that provide information on the number of hours of fishing and average

vessel speed during fishing), together with estimates of the dimensions of the different gear components to calculate the total seabed area swept (km^2) by a fishing gear per annum (for details refer to Hintzen et al. 2012; Eigaard et al. 2015).Fishing pressure is defined as the number of times an area is swept by bottom gear in a year (km^2 swept km^{-2} seabed), and is hereafter referred to as fishing frequency. Owing to the exemption of vessels smaller than 15 m from the VMS reporting process of positional information, the estimates of fishing frequency may be underestimates of the actual fishing intensity, however these are still useful indicators of the relative fishing pressure at the sampled sites.

Sampling of invertebrate populations and sediment biogeochemistry

Three sediment cores with overlying water were collected at random locations within each sampling site using a 0.1 m^2 NIOZ (Netherlands Institute for Sea Research, Texel) corer. The corer (30 cm internal diameter) collected sediment to a maximum depth of 50 cm, depending on sediment hardness. Only intact cores with overlying water were used, as drainage of water would disturb biogeochemical profiles. Oxygen profile readings and pore-water nutrient samples were collected from one of the three cores collected at each sampling site, chlorophyll *a* (Chl *a*) and organic carbon and nitrogen content were determined for two replicate cores and sediment particle size analysis (PSA) and infauna composition from all three cores.

Oxygen profiles

To measure benthic oxygen status, a 10 cm wide by 30 cm long sediment Perspex sub-core was sampled from the NIOZ core to collect sediment together with the overlying water. Sediment oxygen concentration profiles were measured immediately after collection using Clarke-type oxygen microelectrodes from Unisense (Revsbech 1989). Two profiles were taken for each sub-core. The oxygen penetration depth (OPD), which is the depth to which free oxygen is present in the sediment, was estimated as the deepest depth at which oxygen saturation above 0% was observed using a method adapted from Rabouille et al. (2003).

Particle size analysis (PSA), porosity, Chl *a* and organic carbon analysis

Five centimeter diameter sediment sub-cores were collected for PSA and for porosity, Chl *a* and organic carbon and nitrogen analysis. Sub-cores were frozen at −20°C upon collection and transported to the laboratory for analysis. A combination of dry sieving and laser diffraction techniques were used to produce a complete particle size distribution for sediment particles larger and smaller than 1 mm, respectively. Porosity was calculated following methods described by Holme and McIntyre (1984). Sediment Chl *a* was extracted from the thawed sub-cores using acetone and analysed using a fluorometer as described by Tett (1987). Samples for the analysis of sediment organic carbon and nitrogen were thawed, freeze dried and acidified as described in Hedges and Stern (1984). Organic carbon and nitrogen content was then determined using a Thermo-Finnigan elemental analyser.

Pore-water nutrient profile data

Samples for pore-water nutrients were extracted using a sipping system from intact NIOZ cores at the following sediment depths; 0, 1, 2, 3, 4, 5, 7.5, 10, 14, 17, 20 cm (D. B. Sivyer, unpubl.). The extracted water samples were filtered using 0.2 μm filters and analysed for nitrate, nitrite, ammonium, silicate, and phosphate using a scalar auto-analyser (Kirkwood 1996).At the sandy sites, the deepest pore-water sample was taken at 14 cm as the NIOZ corer generally penetrated to about 15 cm in sand.

Infauna

Following removal of the sub-cores for the non-faunal sediment samples (above), the rest of the core sample was sieved over a 1 mm sieve and the benthic invertebrates collected were fixed and preserved in 4% formaldehyde solution for subsequent identification. In the laboratory, all invertebrates were identified to the highest practicable taxonomic resolution (mostly species) and the wet weight of each individual organism was measured after blotting.

The sediment within the sub-core used for oxygen measurements (ca. 0.16 m^3, equivalent to ca. 35% of the total core sample) was also sieved over a 1 mm sieve and the infauna preserved in 4% formaldehyde solution. However, the volume of sediment removed for PSA, Chl *a*, porosity and organic carbon and nitrogen was small (0.018 m^3, equivalent to ca. 4% of total core sample) and was assumed to have negligible contribution to overall infauna abundance and biomass. Furthermore, the freezing and thawing process damages animal tissue hence making the process of species identification difficult. Therefore, sediment sub-samples collected for PSA, Chl *a*, porosity and organic carbon and nitrogen were not processed for infauna.

Sediment Profile Images

A Sediment Profile Imagery (SPI) camera was deployed five times at each station to obtain estimates of the depth of the apparent redox potential discontinuity (aRPD) layer, which is the depth at which the sediment transitions from an oxidising to a reducing environment, as determined by the Fe^{3+}/Fe^{2+} colour boundary. Penetration depth (the depth that the SPI prism had penetrated the sediment surface) and the depth of the aRPD layer were measured from the images using the NIH software ImageJ as described in Teal et al. (2010).

Analyses

Environmental conditions at the sampling sites

Station characteristics were reviewed after the survey with the most up to date fishing frequency estimates and actual sediment composition information collected during the survey (PSA and water depth data). Multi-Dimensional Scaling

(MDS) of normalized environmental variables (% sand, % mud, water depth, tide stress, and wave stress) was used to exclude outlier stations in terms of the environmental variables examined. Further, we carried out correlation tests using Pearson's coefficient to identify sites that contributed to a significant correlation between fishing frequency and each of the environmental variables mentioned above. These sites were removed to avoid confounding the effect of fishing with that of other environmental variables. Out of a total of 32 sites that were sampled during the survey, 19 sites were retained for statistical analyses; 11 sites from the muddy study area and 8 sites from the sandy area. The environmental parameters (water depth, tide and wave bed stress, % sediment grain size composition) at these 19 stations were not significantly correlated to fishing frequency (see Supporting Information SM 2).

Effect of fishing on faunal parameters

Analyses exploring the relationship between different faunal parameters (total infaunal density and biomass, species trait-specific biomass) and fishing frequency (yr^{-1}) were performed using General Linear Models (glm package) in R v.3.0.3. A Gaussian error distribution was used for each model. Homogeneity of residuals was established through visual examination of plotted standardized residuals vs. fitted values. Data was log-transformed whenever homogeneity of variance was violated. Mean and standard error value (Mean ± SE) are provided throughout the text.

The community bioturbation potential (BP_C), first described by Solan et al. (2004), was used to estimate how the potential of the benthic assemblages to regulate ecosystem processes through their sediment reworking activities is influenced by fishing. This metric combines abundance (A_i) and biomass (B_i) with information about the behavioural traits of individual species that are known to regulate biological sediment mixing; R_i describes modes of sediment reworking and M_i describes levels of motility of the taxa in the assemblage (Solan et al. 2004). Values for R_i and M_i were obtained from Queiros et al. (2013). The community bioturbation potential, $BP_{C,}$ was calculated as follows (Queiros et al. 2013):

$$BP_C = \sum_{i=1}^{n} \sqrt{\frac{B_i}{A_i}} \times A_i \times M_i \times R_i$$

Additionally, the influence of fishing on species with different biological traits was examined. Three traits that may influence the vulnerability of species to fishing or influence sediment processes (e.g., nutrient cycling) through changes in macrofauna composition and/or abundance were selected, namely feeding mode, mobility and mode of bioturbation. "Modalities" within each trait were chosen to encompass the range of possible attributes of all the taxa; for example, modalities for mobility were "swimming," "burrowing," "crawling," and "sessile." A full description of the modalities within each trait category is given in Supporting Information SM 3. Traits information was obtained from the biological traits database generated from the BENTHIS project (Bolam et al. 2014*b*, http://www.benthis.eu/en/benthis/Results.htm, accessed 25 September 2015). The biomass of species within each trait and modality class was summed to obtain the total biomass of organisms within the different modalities (e.g., total biomass of sessile species). A GLM model with interaction [log(biomass) ~ fishing × modality] was fitted for each of these traits to assess how the response to fishing disturbance changes among species with different trait characteristics.

Effect of fishing on biogeochemical parameters

The effect of fishing on the bulk biogeochemical properties of the upper 5 cm of the sediment (Chl *a*, organic carbon and nitrogen content, porosity, OPD, and aRPD) was examined using General Linear Models (GLMs). Pore-water nutrient profile concentrations were integrated into three depth categories that represent the observed general zonation in sediment chemistry due to natural (i.e., macrofauna) and anthropogenic (i.e., bottom fishing) factors. While we acknowledge that oxidation zones will be shallower in mud and potentially deeper in sand, we use similar zone intervals across the two sediment types for comparability across the regions and sediment types. We use a generic conceptual zonation pattern (rather than site-specific zonation) to illustrate broad differences in the effect of fishing on different depth zone-related processes in the two sediment types. We believe that findings from this approach have wider generalizability and applicability than a site-specific approach. The depth categories examined were as follows: (i) 0–2 cm: according to the OPD and aRPD measurements at the study sites this is predominantly the *oxic* zone where there is still free oxygen which acts as the electron acceptor and where oxidation of ammonium (NH_4^+) to nitrate (NO_3^-) leads to low concentration of NH_4^+ in this layer. Changes in this zone may be driven by faunal respiration (as seen in OPD data), organic matter input or sediment resuspension or mixing due to fishing; (ii) 2–5 cm: *anoxic/suboxic* zone where free oxygen is no longer available and organic matter breakdown is through NO_3^-, manganese (Mn) and iron (Fe) cycles. Denitrification processes result in low concentration of TOxN (Total Oxidised Nitrogen—NO_3^- and NO_2^-) but organic matter breakdown can induce higher NH_4^+ in this layer. Fishing is likely to affect the biogeochemistry of the sediment at this depth by removing and/or reducing macrofauna that play a critical role in sediment mixing and often linked to the aRPD or Biological Mixing Depth (BMD); (iii) 5–20 cm: *fully anoxic* zone where oxygen is depleted and sulphate (SO_4^{2-}) is mainly used as the electron acceptor. NO_3^- concentration in pore-water is low at these depths but NH_4^+ increases as a result of organic matter degradation in a reducing environment. Bottom fishing may have an effect on the

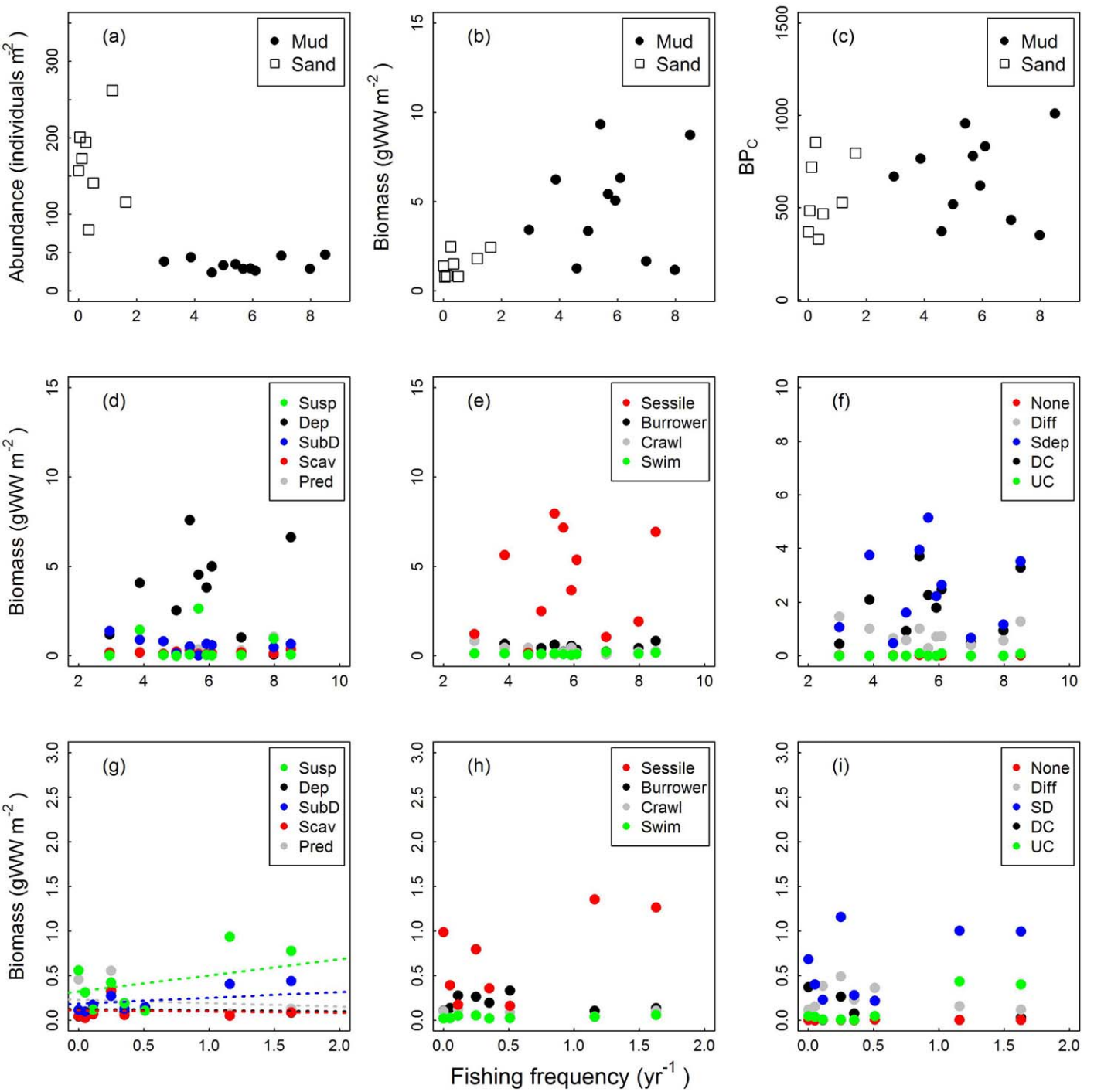

Fig. 2. The effect of bottom fishing on (a) total infaunal abundance, (b) total infaunal biomass (grams wet weight, g WW), (c) community bioturbation potential (BP_C) and on the biomass of species with different feeding modes, mobility and modes of bioturbation in mud (d–f) and sand (g–i). The dotted lines represent GLM models for significant effects of fishing on different trait modalities. [Feeding modes: Susp, suspension feeder; Dep, deposit feeder; SubD, subsurface deposit feeder; Scav, scavenger; Pred, predator. Mobility: sessile, burrower, crawler, swimmer. Bioturbation mode: None, non-bioturbating organism; Diff, diffusor; Sdep, surface deposition; DC, downwards conveyor; UC, upwards conveyor].

biogeochemistry in this zone by increasing organic matter supply by sediment and carbon burial to depth. Macrofaunal influences are expected to be minimal at this zone because the sediment is too anoxic for most macrofauna to survive, unless they are deep sediment burrowers. GLM models with interaction [log(nutrient concentration) ~ fishing × depth zone] were examined for each of the nutrients to assess how the response to fishing disturbance changes with sediment depth.

Table 1. Statistical outputs of the general linear models (GLMs) examining the relationship between the biomass of species with different biological traits (modality) and fishing frequency (yr^{-1}) (fishing) in mud. "Fishing × modality" refers to the interaction term of the GLM. Significant relationships are shown in bold. df (*x*,*y*) indicates model and residual degrees of freedom, *F* is the *F*-statistic for the GLM model.

Mud: *Nephrops* fishing ground			
a. Feeding mode	df	*F*	*p*
Fishing	1,45	0.16	0.69
Modality	4,45	11.76	**<0.0001**
Fishing × modality	4,45	0.34	0.85
b. Mobility	df	*F*	*p*
Fishing	1,36	0.16	0.69
Modality	3,36	17.90	**<0.0001**
Fishing × modality	3,36	0.44	0.72
c. Bioturbation mode	df	*F*	*p*
Fishing	1,45	0.31	0.58
Modality	4,45	14.08	**< 0.0001**
Fishing × modality	4,45	0.37	0.83

Table 2. Statistical outputs of the general linear models (GLMs) examining the relationship between the biomass of species with different biological traits (modality) and fishing frequency (yr^{-1}) (fishing) in sand. "Fishing × modality" refers to the interaction term of the GLM. Significant relationships are shown in bold.

Sand: Isle of Man fishing ground			
a. Feeding mode	df	*F*	*p*
Fishing	1,30	2.39	0.13
Modality	4,30	5.13	**0.003**
Fishing × modality	4,30	2.93	**0.04**
b. Mobility	df	*F*	*p*
Fishing	1,24	1.22	0.28
Modality	3,24	10.03	**0.0002**
Fishing × modality	3,24	2.62	0.07
c. Bioturbation mode	df	*F*	*p*
Fishing	1,30	1.78	0.19
Modality	4,30	11.32	**<0.0001**
Fishing × modality	4,30	1.60	0.20

Direct statistical comparisons of the relationship between response and predictor variable in mud and sand was not attempted as the overlap in the range of fishing frequencies between the two study areas was only limited. All analyses were based on the mean values for each variable at each sampling site.

Results

The muddy sites were composed of more than 60% mud (<63 μm) and the sediment was poorly sorted, whereas the sandy sites were composed of more than 95% sand (>63 μm and < 2000 μm) and the sediment was moderately well sorted (Supporting Information SM 1). The fishing frequencies between the two study areas did not overlap; the fishing frequency ranged from 2.95 yr^{-1} to 8.51 yr^{-1} at the muddy sites and from 0 yr^{-1} to 1.63 yr^{-1} at the sandy sites (Supporting Information SM 1).

Effect of fishing on faunal parameters

There was no significant effect of fishing on total infaunal abundance or biomass in either mud (abundance: $t = 0.39$, df = 9, $p = 0.71$, $r^2 = 0.02$; biomass: $t = 0.27$, df = 9, $p = 0.79$, $r^2 = 0.01$) or sand (abundance: $t < 0.001$, df = 6, $p = 0.99$, $r^2 < 0.001$; biomass: $t = 1.73$, df = 6, $p = 0.13$, $r^2 = 0.33$) (Fig. 2a,b). The infaunal community in mud was dominated by fewer species but larger individuals, whereas the sand community was characterized by a more diverse assemblage of smaller individuals. The average total infaunal density and biomass in sand were 198.14 ± 27.14 individuals m^{-2} and 1.54 ± 0.29 g WW m^{-2}, respectively (Fig. 2a,b). In mud, the average infaunal density and biomass were 34.69 ± 2.46 individuals m^{-2} and 5.29 ± 0.99 g WW $m^{-2,}$ respectively (Fig. 2a,b). The community bioturbation potential index (BP_C) was similar between the two sediment types and did not change significantly with fishing frequency in mud ($t = 0.12$, df = 9, $p = 0.90$, $r^2 = 0.01$) and sand ($t = 0.88$, df = 6, $p = 0.41$, $r^2 = 0.11$) (Fig. 2c). However, different sediment reworking functional groups dominated the community in sand and mud; regenerator and biodiffusor species such as the polychaetes *Maxmuelleria lankesteri* and *Nephtys incisa*, and the malacostracan *Callianassa subterranea* dominated the total community biomass at the muddy sites, whereas surficial modifiers such as the bivalves *Lucinoma borealis* and *Ensis ensis*, the echinoderms *Astropecten irregularis* and *Labidoplax* sp. and the phoronid *Phoronis* sp. dominated the total community biomass at the sandy sites (Supporting Information SM 4). An assessment of the effect of fishing frequency on infaunal community composition using either species density or biomass data did not reveal any significant relationships between fishing and the biotic community in either mud or sand (Mud: $F_{[1,10]} = 1.05$, $p = 0.38$, $r^2 = 0.10$; Sand: $F_{[1,7]} = 1.58$, $p = 0.11$, $r^2 = 0.20$).

Sessile species (3.96 ± 0.80 g m^{-2}) and deposit feeding organisms (3.32 ± 0.77 g m^{-2}) had significantly higher biomass than species with other motilities and feeding strategies in mud (Fig. 2d,e; significant "Modality term" in Table 1a, b). However, none of the motility, feeding or bioturbation modalities examined at the muddy sites showed a significant relationship with fishing frequency (non-significant "fishing term" in Table 1). In contrast, fishing resulted in a significant increase in the biomass of surface deposit feeders and suspension feeders relative to predators and scavengers at the sandy sites (Fig. 2g; significant "interaction term" in

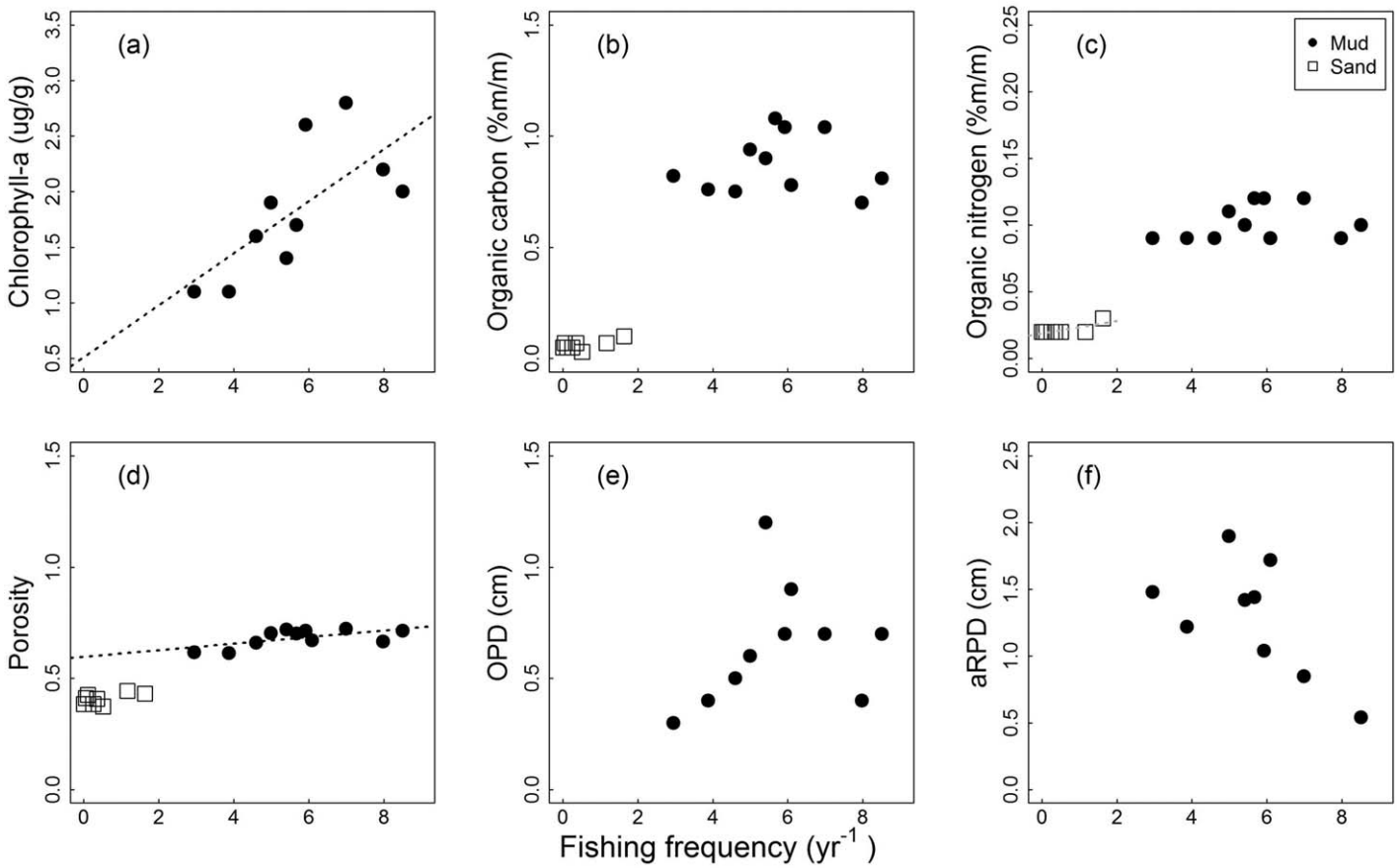

Fig. 3. The effect of bottom fishing on biogeochemical parameters in mud (black symbols) and sand (grey symbols): (a) sediment Chl *a* content, (b) organic carbon content, (c) organic nitrogen content, (d) sediment porosity, (e) maximum oxygen penetration depth (OPD) in cm, (f) apparent redox discontinuity layer (aRPD) in cm. The dotted line represents the GLM model for significant effect of fishing (see results text for data on sediment Chl *a*, aRPD and OPD in sand).

Table 2a). There was no significant effect of fishing on species with different mobilities or bioturbation modes in sand (Table 2b, c).

Fishing impact on biogeochemical parameters

The sediment at the muddy sites had significantly higher organic carbon and nitrogen content than the sandy sites (organic carbon: $0.87 \pm 0.04\%$ m/m in mud vs. $0.06 \pm 0.01\%$ m/m in sand; organic nitrogen: $0.1 \pm 0.004\%$ m/m in mud vs. $0.02 \pm 0.001\%$ m/m in sand) (Fig. 3b,c). The average Chl *a* content of the muddy substratum was 1.8 ± 0.18 μg/g (Fig. 3a), whereas that in sand was < 1 μg/g, which was lower than the minimum detection limit of the fluorometer hence why no data is plotted for sand in Fig. 3a. At the muddy sites, sediment Chl *a* content and porosity increased significantly with fishing frequency indicating that the sediment matrix contained more water and phytodetritus at sites exposed to higher fishing disturbance (Fig. 3a,d; Table 3a). There was a slight but significant increase in organic nitrogen content with fishing frequency at the sandy sites, but no significant effects of fishing on organic carbon content (Table 3b).

The oxygen penetration depth (OPD) and the depth of the apparent redox discontinuity layer (aRPD) were shallower than 2 cm across the sites sampled in the muddy substratum. The OPD ranged between 0.30 cm and 1.20 cm and the aRPD between 0.85 cm and 1.90 cm in mud (Fig. 3e,f). Most of the oxygen profiles showed a smooth decreasing trend in the concentration of free oxygen with sediment depth, indicating that the oxygen distribution in mud was governed by molecular diffusion between the oxic seawater and the oxygen-consuming sediment (Supporting Information SM 5A). Neither the OPD nor the aRPD showed a significant relationship with fishing frequency in mud (Table 3a). The coarse sand mixed with shell fragments at the sandy sites only allowed oxygen profiling of the top 2 cm of the sediment core. High concentrations of oxygen were still present at 2 cm (Supporting Information SM 5B), thus suggesting that the OPD in sand was deeper than 2 cm. In sand, the SPI-camera penetrated to a maximum depth of 6.26 cm (compared to 21.36 cm in mud) and no aRPD layer was

Table 3. Statistical outputs of the GLM models examining the relationship of different biogeochemical parameter to fishing frequency (yr^{-1}) in (a) mud and (b) sand. Significant relationships are shown in bold. *t* and SE indicate the *t*-statistic and the standard error for the GLM model, aRPD is the apparent redox discontinuity layer, OPD is the oxygen penetration depth.

Biogeochemical parameter	Slope	SE	*t*	*p*	adj-r^2
(a) Mud: *Nephrops* fishing ground					
Organic carbon (%m/m)	0.01	0.03	0.09	0.93	0.001
Organic nitrogen (%m/m)	0.01	0.01	0.73	0.49	0.001
Chl *a* (μg/g)	**0.23**	**0.08**	**2.80**	**0.02**	**0.43**
Porosity	**0.01**	**0.01**	**2.35**	**0.04**	**0.31**
aRPD (cm)	−0.16	0.08	−2.08	0.08	0.29
OPD (cm)	0.04	0.05	0.85	0.42	0.001
(b) Sand: Isle of Man fishing ground					
Organic carbon (%m/m)	0.02	0.01	2.15	0.07	0.34
Organic nitrogen (%m/m)	**0.005**	**0.002**	**2.98**	**0.02**	**0.53**
Porosity	0.02	0.01	1.71	0.14	0.22

visible, thus suggesting that the aRPD in sand was deeper than 6 cm. A subset of SPI-images is presented in Supporting Information SM 6 to illustrate the different nature of the sediments at the two study sites. The lack of an obvious colour stratification together with a visible fluff layer in most of the SPI-images obtained from the muddy sites indicate that the sediment is highly disturbed at these sites (Supporting Information SM 6).

The concentrations of ammonium (NH_4^+) and silicate (SiO_4^-) in pore-water were an order of magnitude higher in mud than in sand (Fig. 4, Supporting Information SM 5), reflecting the higher organic carbon and Chl *a* (and associated diatom) levels in mud, which are the source of these inorganic nutrients. The integrated-depth profiles for NH_4^+ in mud (Fig. 4a) shows significantly higher concentrations of NH_4^+ in sediment deeper than 2 cm (48.13 ± 17.72 μmols/L) than in the upper 2 cm of the sediment (24.43 ± 19.04 μmols/L) (significant "Depth zone" term in Table 4a). The concentration of NH_4^+ and SiO_4^- decreased significantly with fishing frequency within the top 2 cm of the muddy sediment, but increased significantly with fishing between 5 cm and 20 cm (Fig. 4a,c; significant interaction term in Table 4a, c). Phosphate (PO_4^{3-}) concentrations were similar across all depth zones in mud, and did not show any significant effect of fishing (Fig. 4b; Table 4b). The concentration of NH_4^+, SiO_4^-, and PO_4^{3-} in the upper 5 cm were consistently low at the sandy sites, indicating higher pore-water flow between the sediment and water column and an upper mobile well-oxygenated sediment layer that is typical of sand but not of mud (Fig. 4d–f). NH_4^+ and PO_4^{3-} showed an overall small but significant increase in concentration with fishing frequency. However we found no significant interaction effect of fishing and depth zone suggesting a homogeneous effect of fishing with depth (Table 4a, b).

Discussion

Our assessment of the effects of bottom fishing disturbance on the infauna and biogeochemical properties of soft sediments revealed some effects of bottom fishing on benthic biogeochemical processes, but these effects differed between mud and sand. Scallop dredging on sand had little effect on the infauna and sediment biogeochemistry; other factors such as tidal currents and waves might play a role in regulating the biogeochemical processes in this hydrodynamic environment. Several studies have shown that bottom currents generated by tides and waves play an important role in transporting interstitial water into and out of highly permeable sediments such as sands (Huettel et al. 1996; Huettel and Webster 2001; Ehrenhauss et al. 2004). In contrast, otter trawling on mud increased sediment Chl *a*, porosity, the concentration of NH_4^+ in the pore-water deeper than 5 cm and decreased the concentration of NH_4^+ in the top 2 cm. These observations point toward a number of possible mechanisms through which trawling may be impacting organic matter remineralization and nutrient cycling in mud. First, otter trawling may be resuspending sediment in the upper (0–2 cm) sediment layers, which acts to decrease the pore-water concentrations of nutrients typically generated at depth (e.g., NH_4^+) as these are lost to the overlying water column. Bobbins and chains scrape off surface sediment layers, causing the redistribution of both sediment particles and nutrients as they are dragged along the seabed (Jones 1992). Second, otter trawling may be burying organic matter to deeper sediment, which acts to increase NH_4^+ production at depth (beyond 5 cm) as organic matter is broken down under anaerobic conditions. Otter boards leave distinct tracks on the seafloor, ploughing grooves which can vary from a few cm down to 35 cm in muds (Eigaard et al. 2015). Therefore, it is likely that the increase in NH_4^+ production at the depths observed at the muddy sites is due to organic matter burial or mixing to depth by otter board action. Furthermore, the presence of significant pore-water TOxN concentrations below 5 cm at some sites illustrates that there must be significant pore-water relocation caused by trawling, which is the only process which could act to these depths at the sites. The injection of carbon to depth is also likely to stimulate localized Fe reduction which mediates increased phosphate release at depth. Future analysis of total organic carbon and C : N ratios in profiles would enable age determination and source of carbon, hence allowing the mechanism of impact to be identified better.

The elevated concentration of dissolved nutrients released from the sediment could account for the increase in sediment Chl *a* observed at the higher trawling frequency muddy areas (e.g., Sparks-McConkey and Watling 2001).

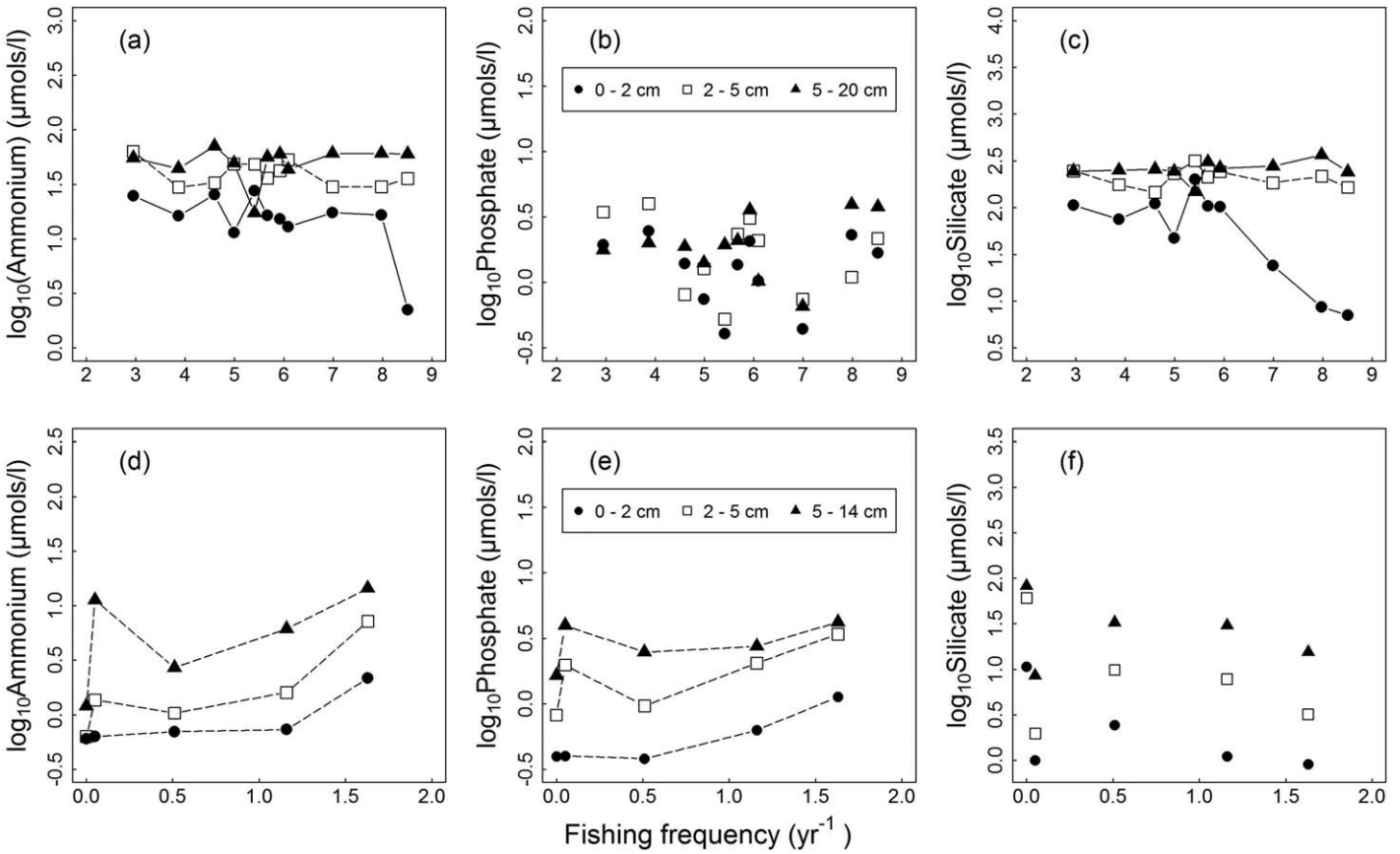

Fig. 4. Depth-integrated ammonium, phosphate, and silicate concentration (log_{10}-transformed) profiles recorded at increasing fishing frequency in mud (a–c) and sand (d–f). The solid line represents the GLM model for significant effect of fishing*depth zone, dotted line represents the GLM model for significant effect of fishing.

However, this is unlikely as the main source of Chl *a* at the muddy area is deposition of phytoplankton rather than generation at source as the amount of light reaching the seabed at the studied sites is negligible (Foden et al. 2008). Furthermore, tidal currents are likely to move any released nutrients over distances larger than the distance between our sampling sites. Benthic macrofauna are known to play an important role in controlling the levels of total organic carbon (TOC) and Chl *a* in the sediment by controlling rates of TOC remineralization (via redox) and phytodetritus incorporation within the sediment via bioturbation processes. For example, in an extensive survey of the North Sea soft sediments, Solan et al. (2012) and R. Parker (unpubl.) found that a decrease in community complexity and bioturbation capacity led to a decrease in sediment oxygenation and carbon cycling which resulted in higher sediment TOC, and a decrease in sediment reworking rates that led to lower Chl *a* concentrations due to lower phytodetritus incorporation within the sediment. We found no significant effect of trawling on infaunal abundance and BP_C at either of the study areas and therefore have no evidence that trawling is affecting the sediment biogeochemistry through changes in macrofaunal composition

Table 4. Statistical output of the GLM models examining the relationship of pore-water nutrient concentrations (log_{10}-transformed) to fishing frequency (yr^{-1}) and sediment depth in mud and sand; Significant model terms are shown in bold. *F* is the *F*-statistic for the GLM model.

	Mud		Sand	
	F	*p*	*F*	*p*
a. $log_{10}(NH_4^+)$				
Fishing	4.24	**0.04**	9.75	**0.01**
Depth zone	26.11	**<0.001**	9.06	**0.01**
Fishing × depth zone	3.45	**0.04**	0.25	0.78
b. $log_{10}(PO_4^{3-})$				
Fishing	0.10	0.75	11.45	**0.01**
Depth zone	1.37	0.27	27.91	**<0.001**
Fishing × depth zone	0.74	0.49	0.62	0.56
c. $log_{10}(SiO_4^-)$				
Fishing	10.89	**0.003**	1.81	0.21
Depth zone	35.26	**<0.001**	6.58	**0.02**
Fishing × depth zone	12.03	**<0.001**	0.16	0.86

and/or loss of bioturbation potential. Alternatively, trawling may lead to a substantial reduction in bacterial biomass as the sediment is resuspended in the water column, hence slowing down the remineralization of the labile portion of organic matter within the sediment. Watling et al. (2001) observed a 50% reduction in microbial biomass after dredging an undisturbed area by commercial scallop dredgers. This reduction is expected to be higher in heavily trawled areas than in lightly trawled areas, hence the higher concentration of Chl *a* observed at higher trawling frequency areas. It is well acknowledged that a lot of the nutrient cycling and flux is linked to the microbial activity within the sediment (Snelgrove 1997; Friedrich et al. 2002; Tait et al. 2014). Future examination of the microbial sediment community in areas with different fishing pressure would improve our understanding in this regard.

Previous surveys from 2003 and 2004 at sites within the muddy area found significant decreases in both infaunal abundance and biomass with increasing trawling frequencies (Queiros et al. 2006; Hinz et al. 2009). Particularly striking between these older surveys and the present survey is the absence of *Amphiura filiformis* from the latter. *A. filiformis* dominated the community biomass (64.13%) in surveys from 10 yr ago, whereas burrowing shrimps such as *Callianassa subterranea*, *Upogebia deltaura* and *Jaxea nocturna* were among the species that dominated the biomass in the present study. Large quantities of suspended sediments (such as those generated by trawling) are known to inhibit the growth of *A. filiformis* but not that of the burrowing mud shrimps (Amaro 2005). The sustained high trawling frequencies over the years at this area may thus be having long-term changes in community composition. The lack of detection of an effect of trawling on infaunal biomass (and any associated changes in biogeochemistry) in this study is more likely to be due to the lack of a true zero (lowest fishing frequency was 3 yr^{-1}) rather than of no effect of trawling. Queiros et al. (2006) recorded a change in body size spectrum at the muddy area; from lots of large and small size classes in lightly trawled area (0.1 yr^{-1}) to a decrease in biomass across the entire size range for more heavily trawled areas (3.5 yr^{-1}). We recognize that our study at the muddy area would have benefitted from having a true control (i.e., areas of no fishing). However, these sites were hard to find as sites with very low or no fishing were characterized by different habitat conditions (sediment composition, tide, and wave stress) from sites where fishing occurred.

A number of limitations associated with the use of fishing pressure indices estimated from VMS data records should be borne in mind for the interpretation of the effects of fishing on the sediment properties and the infauna obtained in this study. First, is the mismatch of spatial scales between the VMS data (km^2) and the sampling gear (m^2), which creates difficulty in determining the exact magnitude of disturbance experienced by the community at the sampled sites. Second, is the temporal variability in the spatial distribution of the fishing fleet from year to year such that the frequency of disturbance at the areas surveyed may differ between years and between sampling sites. Third, is the difficulty of obtaining high resolution VMS data (often withheld from the scientific community for confidentiality reasons, Hinz et al. 2013), which may be used to determine the last fishing disturbance event relative to the benthic sampling event and recovery times of the infauna and biogeochemical processes. The infauna are expected to recover over longer time-scales than the sediment biogeochemical properties, as the former depends on recolonization processes such as larval dispersal and post-larval growth and immigration, which take longer to occur. These discrepancies in spatial and temporal scale between fishing pressure estimates and that truly experienced by the community at the time of sampling might have reduced our ability to detect small-scale or subtle changes in the biota and biogeochemistry at the sampled sites. Future controlled BACI studies with multiple sampling times after the disturbance event would help to address these limitations.

In conclusion, this study has found some effects of bottom trawling on biogeochemistry and infauna on mud but not on sand, where the biogeochemistry appeared to be more strongly influenced by tidal currents and waves. Our first hypothesis that fishing will negatively affect benthic invertebrate abundance and reduce the bioturbation potential was therefore not supported. Our second hypothesis that fishing results in changes in the sediment redox and associated biogeochemistry as a result of sediment resuspension and sediment/carbon mixing to depth as was only partly supported as we did not find an increase in the oxygen penetration depth and higher NO_x in pore-water with increasing fishing, but did find a lower concentration of NH_4^+ and SiO_4^- with increasing fishing frequency within the top 2 cm of the sediment and a higher concentration at >5 cm depth on mud. Our third hypothesis that changes in sediment biogeochemistry due to fishing are larger in mud where macrofauna-mediated processes are expected to play a more significant role than in sand where physical processes such as tides and currents generally mediate the redox system, was partly supported, as we did find larger changes in mud than in sand, but only little evidence that this was mediated by macrofauna. This suggests that otter trawling may be affecting organic-matter remineralization and nutrient cycling through sediment resuspension and burial of organic matter to depth rather than through the loss of bioturbation potential of the benthic community. Under the Marine Strategy Framework Directive (MSFD), European countries are committed to achieve good environmental status (GES) by 2020 (Anon 2008, http://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32008L0056, accessed 11 November 2015). GES requires that both benthic communities and ecosystem processes and functions are not adversely affected by

anthropogenic activities (descriptor 6, seafloor integrity) (Rice et al. 2012). These results imply that management of otter trawling activities on muddy sediments may be more important for maintaining GES of the seabed than management of scallop dredging on sand.

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